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INTRACORTICAL INTERACTIONS IN VISUAL PROCESSING

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FINAL REPORT:

INTRACORTICAL INTERACTIONS

IN

VISUAL PROCESSING

Contract #N62269-83-M-3126

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SUMMARY

Microelectrodes were used to record responses from single cells in the visual system of cats, at the level of the visual cortex. Interactions were discovered and measured between the cell under study and neighboring cells, when these neighbors were stimulated with large patterns. The interactions obey specific rules. It is argued that these rules are ideal for separating and strengthening the neural response to one object from the response of myriad other neurons to a cluttered background. The next step in this project will be multi-electrode array studies to isolate and identify the neurons participating in these interactions.

INTRODUCTION

Images must be processed

Target identification. The use of ever-shorter wavelengths and new techniques such as synthetic aperture side looking radar have made image information widely available. These images must be processed; processing must produce identification. Until now, image processing for identification has been elementary. Systems have simply found the brightest point in the field, as in heat seeking devices. Laser locator and designator systems are not very different: a laser turns any object into the brightest point in the field. It is an advantage that now a human operator can contribute some identification work for selecting one target, but progress has not been made in automating identification nor in dealing with multiple targets.

In specific point reconnaissance, particularly for targeting and retargeting, there has been a trend away from simply finding the brightest point in the field toward natural-image target identification. This has brought to the fore problems arising from multiple targets and highly cluttered backgrounds.

Figure/ground segregation. Coincidentally, these concerns are similar to problems now confronting visual science. In pursuing the basis in brain of visual perception, much is understood of the responses of single cells to isolated lines and edges. But lines are not isolated in everyday visual scenes. Further, objects are large enough to excite large populations of neurons. The response from such a population must be synthesized or combined in some way to create the neural representation of an object, and background responses must be suppressed. Combining and suppressing mechanisms must be discovered if we are to grasp how a response to an object is separated from responses to a cluttered background, and subsequently how the object is identified.

Goals of project. In broadest terms, the goal of this project was the discovery of neural interactions which could serve as the combining and suppressing mechanisms of figure/ground segregation.

Neural interactions which can serve as the basis of figure synthesis are the key to pattern recognition. Figure synthesis--the "pattern" part of pattern recognition--and identification/recognition take part in separate brain areas. In order to get the information which must be transmitted from one cortical area to another down to manageable proportions, the object of interest which is fixated in our glance must be separated from the background. Its neural representation can then be sent elsewhere for identification. For the brain, it is uneconomical and biologically impossible to project the entire visual array--the map of activity for the entire visual field--from one area to another, while for us, imagining that this is done only postpones confronting the problems of image processing. Among the many visual areas and

parallel paths running between them, there will be one area concerned with putting the parts of an object together and discarding the rest of the visual response. This area is where the path to conscious pattern recognition begins.

Position invariance.

Figure-ground segregation itself solves an important problem while preparing image information for identification. That problem is position invariance. Suppose a visual field containing a target is imaged on a sensor array, and the target is identified. This identification should "stay put" when the target moves to new positions. This is position invariance. Two things are needed for position invariance. First, the sensor array must be able to isolate the response to the target and discard all other activity. This is figure-ground segregation. Second, the sensor array must converge onto the identification area. This simple arrangement solves the position invariance problem: the upstream identification area will receive the same "object" signals wherever the object is imaged on the downstream sensor array.

Intracortical facilitation. A specific project goal was to find evidence for intracortical facilitation. Intracortical facilitation is important for figure synthesis. Facilitation by definition enables an active unit to increase the responsiveness of another unit. Is this facilitation selective? Orientation, spatial position, movement direction and other cues are known to be important stimulus dimensions for visual cortex. Information about these stimulus attributes is well represented neurally. Whether facilitation is selective with regard to these dimensions is a very practical question. Consider the edge of a book or a building. The edge is long enough to stimulate hundreds of single units, and the nature of the visual world guarantees these these neurons will have something in common: they will share the same orientation preference, and their receptive fields will be lined up edge-to-edge across the visual field. Statistically, units responding to a single object are likely to have certain attributes such as these in common. These common attributes must be used to tie the units together. My hypothesis was that units with such co-axially aligned, co-oriented receptive fields would be mutually facilitatory.

Experiments performed

Facilitation was studied in isolation from the responses of classic receptive field areas. To do this, the large stimuli used to stimulate neurons surrounding the unit under test were shielded from falling upon the receptive field of the test neuron. These stimuli are referred to as contour adapting fields. This approach maximizes the chances that effects observed are intracortical. Special properties of the facilitation, if any, may be isolated in bold relief.

Rapid means of delimiting the classic receptive field were developed. Only with the limits of the receptive field accurately known can the neuron be shielded from direct stimulation by the adapting field. The chief tests for receptive field size were length-response curves and response profiles obtained against activated discharge. "Activated discharge" refers to an artificially elevated, steady response level. This response provides a background against which inhibitory receptive field areas may be seen. It is produced simply by placing a small, optimal bar on the test neuron's receptive field and keeping that bar in constant motion.

Once isolated, intracortical inhibition and facilitation were studied for orientation tuning and position of origin. These experiments fulfill the project's original goals.

Anatomical substrate

Long & selective interconnections. Recent anatomical findings provide a basis for selective intracortical interactions. This makes a search for functional evidence of such interactions more urgent. The anatomical findings are based on new cell marking techniques. These techniques have revealed intrinsic fibers in visual cortex of surprising extent and regularity of structure. The individual axon may be over 4 mm long, with arborizations clustered at intervals of 0.7 to 1.0 mm (Gilbert & Wiesel, 1983), suggestive of the spacing of cortical columnar systems. When a group of neurons take up HRP from a local injection, a lattice-like pattern of labeling appears, thinning out into isolated patches more remote from the injection site (Rockland & Lund, 1983; 1982). These fibers are a possible substrate for the interactions needed for figure synthesis and figure/ground segregation.

Mitchison and Crick (1982) have shown by computer simulation that patchiness and banding will occur if intrinsic innervations are selective for orientation in a tissue possessing columnar organization. Such selectivity of innervation is important for figure synthesis. The neurons lying outside the marked bands or patches might not participate in a system of selective innervation (Rockland and Lund, 1983), or might follow different rules. It is presently of great interest to establish what the rules of selective innervation might be. Mitchison and Crick (1982) suggested two possibilities. In both, cells with similar orientation tunings preferentially innervate each other, but the rule for traversing the spatial domain varies. In the first variation, the spatial domain is traversed in a visuotopic direction at right angles to the optimal orientation tuning, while in the second, the spatial domain is traversed along the same axis to which the cells are aligned in the orientation domain.

Old receptive fields or new interactions?. The focus of this project is intracortical interactions, for which these intrinsic fibers might provide a structural basis. But the fibers might instead by performing a more elementary function. In the first (orthogonal) case, the fibers might innervate laterally flanking receptive field regions such as inhibitory sidebands. In the second case, with a co-axial traverse of the spatial domain, receptive field regions such as the inhibitory end zones of hypercomplex units are reached. It has in fact been suggested that receptive field regions are built up by these fibers (Mitchison & Crick, 1982; Gilbert & Wiesel, 1983). In this Final Report, length summation far beyond the retinotopic input from the geniculate nucleus is described. This input must therefore be intracortical in origin, arising perhaps from the long axonal fibers. The summation was revealed firstly by measuring length response curves and secondly, by observing a highly specific facilitatory input from remotely presented gratings when the receptive field is covered. The required pathways follow Mitchison and Crick's (1982) co-axial rule, carry facilitation, and are not generating a conventional receptive field region. The question of whether indeed any receptive field region is large enough to require a 4 mm axon is quantitatively discussed.

METHODS

Animal preparation & cell classification

Extracellular recordings were made in the striate cortex of 23 cats. Normally-reared animals were prepared under anaesthesia (halothane in 70:30 N_2O-O_2). Wounds were treated with a topical antibiotic (Neosporin: Calmic Pharmaceuticals) and infiltrated with a long-acting local anaesthetic (Bupivacaine). Following paralysis with gallamine triethiodide (Flaxedil: May & Baker) and artificial respiration, halothane was reduced to 0.25 to 0.5% in accord with the animal's demonstrated tolerance. End-tidal CO_2 was then brought below 3.5% and a craniotomy and durectomy performed over each hemisphere. Halothane was discontinued prior to electrode insertion and experimental recording. Cortisone (Celestone: Shering) was administered prophylactically against cortical oedema, and 200,000 U penicillin mixture (Triplopen: Glaxo-Allenburys) was given on each morning of the experiments, which typically lasted two to four days. Optical quality was maintained with afocal contact lenses, 3 mm artificial pupils and supplementary lenses. Tungsten-in-glass microelectrodes (Levick, 1972) had a 10 u tip protrusion; for other details of preparation and recording see Nelson, et al. (1977).

Cells were classified in the simple or complex families according to the separation or overlapping of the ON and OFF responses to a stationary flashing bar (Hubel & Wiesel, 1962), or, equivalently, the responses to moving light and dark edges. Hypercomplexity (end-stopped inhibition) was observed in either class. B cells were recognized as having mixed ON-OFF response regions but receptive field sizes similar to simple cells (Henry, Lund & Harvey, 1978). The 7 B cells encountered were similar to the 45 simple cells with regard to the properties studied here, and are tabulated with them.

Receptive field mapping & stimulation

Particular care was taken to delimit all receptive field regions using three tests (see Fig. 1). These were 1) a post stimulus time histogram (**PSTH**) taken for a bar of optimal orientation in the presence of activated discharge (Fig. 1.2; Henry et al., 1969); 2) a length-response curve for a bar of optimal orientation describing response summation as stimulus bar length is increased (Fig. 1.1); and 3) an activated discharge profile taken with the bar at 90 deg to optimal orientation (Fig. 1.3). The **standard PSTH** gives a profile or cross section of the receptive field. It reveals the width of both the "excitatory discharge center" (Fig. 1, XDC; Bishop et al., 1971) and the inhibitory sidebands flanking it (Fig. 1, black rectangles). The discharge center may have multiple peaks (Bishop et al., 1973; Palmer & Davis, 1981). All profiles were based on 150 to 600 sweeps. The **length-response** curve gives the limits of the discharge center length, and reveals the presence of end-zone or end-stopped inhibitory areas ("hypercomplexity;" Orban et al., 1979a) occurring above and below the discharge center. Length-response curves were measured unilaterally, avoiding possible nonlinear half-field interactions reported (in Area 18) by Hammond & Andrews (1978).

Figure 1 about here.

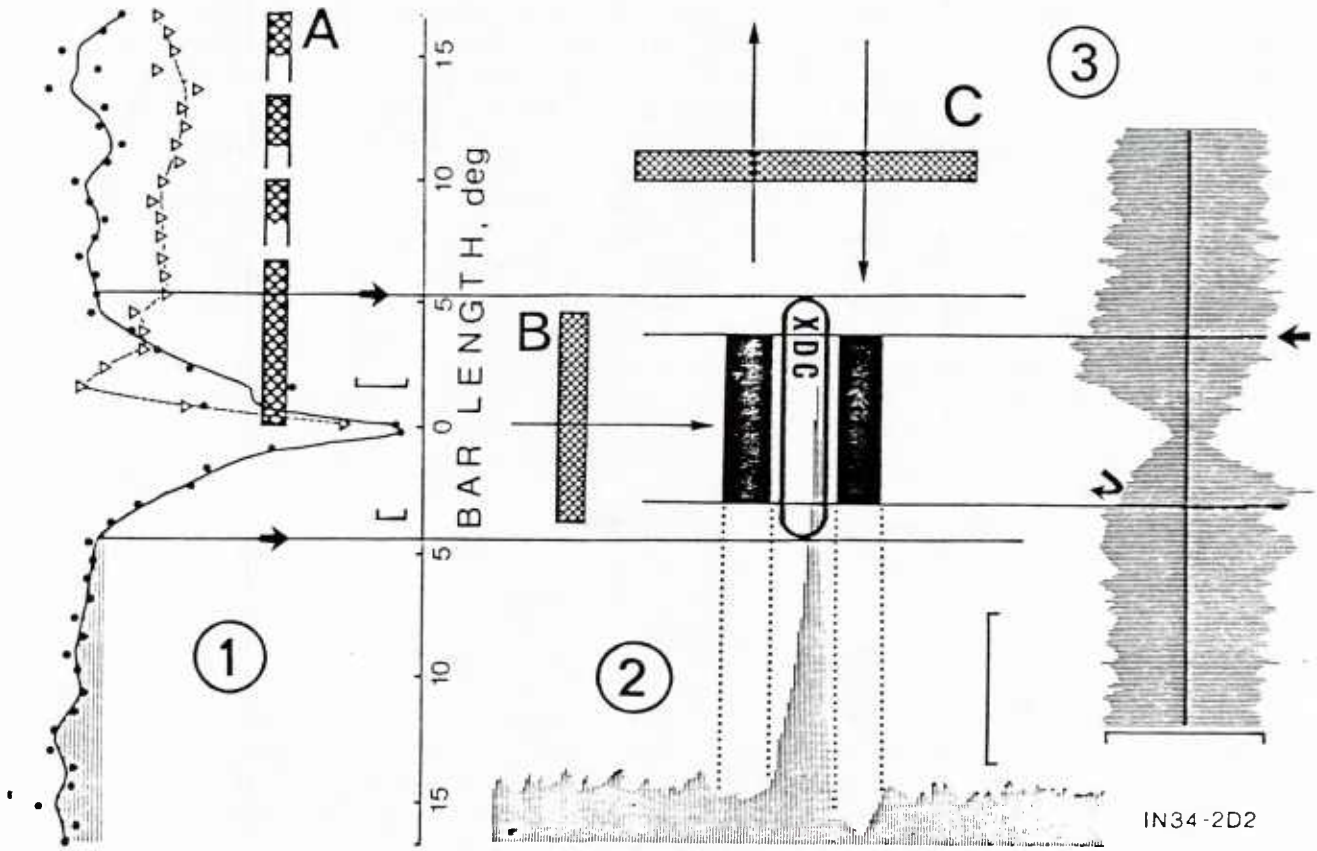

Fig. 1. Components of a cortical simple cell receptive field and three methods used to assess them. 1. The length-response curve is obtained by a bar A of increasing length, beginning as an 0.28 wide x 0.16 deg long slit well-centered upon the receptive field. Separate runs are made with the bar increasing upward and downward (dots, response climbs leftward from the vertical "BAR LENGTH" axis) to reveal possible asymmetry in the receptive field. The shoulders of the length-response curve delimit (arrows) the length of the excitatory discharge center, XDC. The absence of a response decrease beyond this shoulder establishes the absence of end-zone inhibition ("hypercomplexity") above and below the XDC. The length-response curve on the lower left reveals spatial summation extending out to perhaps 14 deg from the receptive field center (shading). A misorientation of the bar by only 15 deg (triangles; this curve is bilateral: both ends of the bar grow at once) not only misses the remote summation, but mis-represents the cell as hypercomplex. The response reduction occurs because the bar intrudes into the inhibitory sidebands. 2. The activated discharge PSTH is obtained with a long, optimally-oriented bar B. A small bar kept constantly moving across the XDC (not illustrated) provides the elevated background discharge against which inhibitory as well as excitatory areas may be revealed. 3. A PSTH with the bar C complementary to the optimal orientation reveals the length of inhibitory sidebands (black rectangles). Calibration bars, 1 spike/sweep. The remote inhibitory and disinhibitory functions shown in Fig. 3B were obtained from this neuron with a circular mask 10 deg in diameter shielding the receptive field from stimulation.

There is no excitatory peak in the **90-deg PSTH** due to orientation selectivity, but because the inhibition in inhibitory sidebands is not orientation selective (Bishop et al., 1973; Orban, et al., 1979b), the 90-deg PSTH reveals the length of the sidebands. Excitation may be elicited in former sideband areas by reversing the contrast of the bar. The excitation is not orientation selective either (Henry et al., 1974), although it is profoundly shaped by the inhibitory sidebands which flank it. In any case, inhibitory areas remain in evidence in the 90 deg PSTH, which may therefore be used to measure their length (e.g., Orban et al., 1979b, Fig. 4).

These measures together show the limits of the receptive field so that peripheral stimulation can be arranged to avoid directly stimulating the neuron under test. Thus it can be said with as much certainty as modern methods permit that peripheral stimulation (a large, rear-projected grating pattern) was presented entirely beyond the receptive field's extent. Stimulus contrast was always less than 67% (background, 12 cd/m^2). The gratings used for peripheral stimulation were always square wave, and always moving; sweep amplitude was always 4 periods, with a light bar centered on the receptive field at mid-sweep. The amount of remote inhibition and possible localization of its regions of origin were revealed as a reduction in the activated discharge elicited by an always-optimal central stimulus. Selectivity in the orientation domain was tested by rotating the peripheral grating.

RESULTS

Large gratings excluded from all conventional receptive field areas produced marked inhibitory effects (remote inhibition), illustrated in Fig. 2A. Response to a small, optimal stimulus is high until an adapting field is presented (first arrow), moving in the non-preferred direction and reversing sweep direction 2 sec later (second arrow). Of interest here is a marked modulation to the passage of the bars of the adapting field impressed upon the average response reduction of 77%.

Figure 2 about here.

Disinhibition

Stimulation of the conventional excitatory discharge center (**XDC**) could cause the observed response modulation. However, the maximum receptive field dimensions, derived from statistical analysis of activated discharge profiles and length-response curves for this neuron, are 2.6 deg width x 3.4 deg length. The mask which shielded the receptive field from stimulation by the grating adapting field was 4 deg in diameter. Therefore neither the conventional excitatory regions nor the flanking inhibitory regions were stimulated. Also arguing against inadvertent center stimulation as a source of the observed facilitation is the observation of greater facilitation with larger receptive field masks (3 vs. 5 deg diameter for the simple cell in Fig. 3A and 5 vs. 8 deg diameter in a B-type cell. The facilitation observed was also spatially distinct from the remote inhibition. The remote inhibitory effect arises isotropically all around the receptive field rather than in a confined axial region. Its spatial integration function spreads less broadly across the visual field.

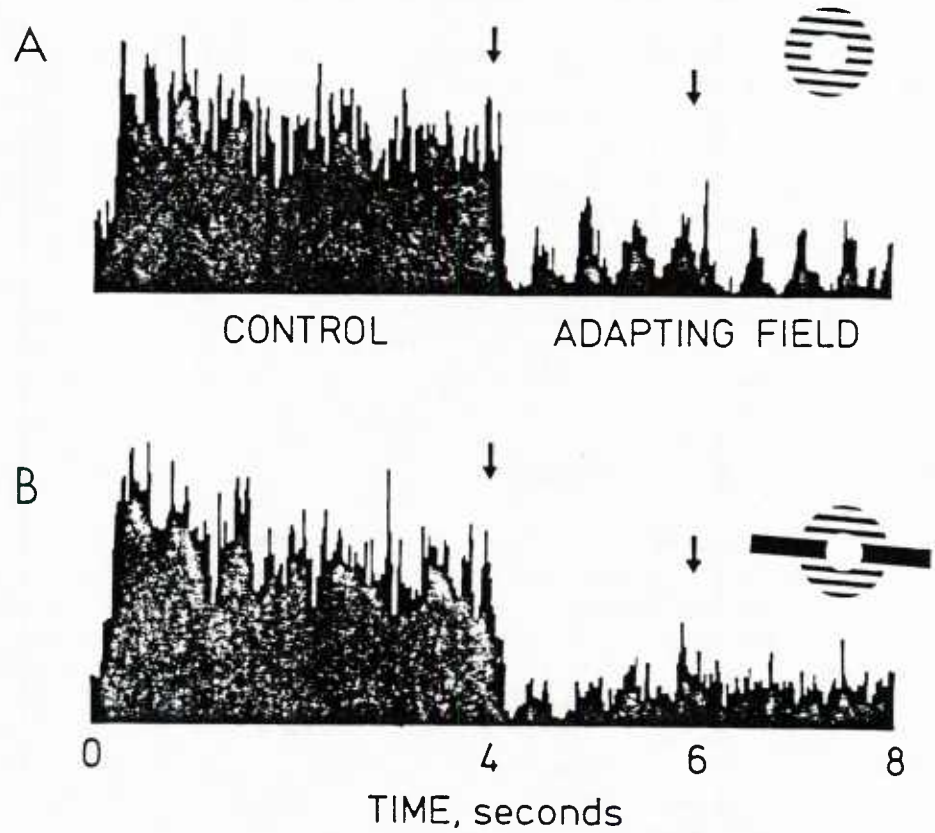

Fig. 2. Periodic relief from inhibition. Receptive field is exposed to a small, optimally-oriented bar but is otherwise masked after being measured as in Fig. 1. Beyond this mask is presented a grating or "contour adapting field" of 0.57 cycles/deg and 21 deg diameter. The half of each histogram labeled "CONTROL" is the response to small bar alone. (A:) Response decreases by 77% when adapting field is presented after 4 seconds (first arrow), moving first in the non-preferred direction and reversing sweep direction 2 sec later (second arrow). Periodic facilitation corresponds to passage of individual stripes across the coaxial extensions of receptive field; it is largely blocked (B) when a 2.5 deg wide, very long opaque strip is placed across receptive field in the neuron's optimal stimulus orientation. Mask, 4 deg diameter; length-response data suggest areas more than 5 deg from the receptive field center contribute to the effect.

Direction selectivity further distinguishes conventional excitation and remote facilitation. The conventional excitatory response of the neuron illustrated in Fig. 2 had a direction selectivity index (difference in preferred and non-preferred direction responses divided by their sum) of 100%, whereas direction selectivity of either the remote inhibition or its modulation is almost nonexistent. Thus, in Fig. 2A the inhibition and the amount of modulation impressed upon it are as great from 4 to 6 seconds when the adapting field (peripheral stimulation) is moving in one direction as it is from 6 to 8 seconds when it moves in the opposite direction. The central XDC responded exclusively to this latter direction.

Similar tests were performed on 40 simple family cells; 17 showed similar modulatory effects, 9 very markedly. Masks were larger than the conventional receptive field regions by similar margins. Direction selectivity differences additionally rule out an origin in unintentional stimulation of the excitatory discharge center in 6 cases. In these neurons, the facilitation (modulation) was observed for both sweep directions of the peripheral stimulation grating while the central excitatory response of the unit under test had greater than 90% direction selectivity. The converse instance of a direction selective remote modulation effect in a bi-directional test unit was observed in 2 cells. Among the cells showing facilitation (modulation) were units satisfying both the X- and Y-innervation criteria of Mustari et al., (1982). Of 11 bimodal cells (two peaks in the receptive field profile), only two showed modulation, although greater attention to optimizing grating spatial frequency and duty cycle (ratio of light to dark stripe widths) with respect to inter-peak spacing might have resolved modulation in a greater proportion of multimodal units.

To further test my impression that the origin of the modulatory/facilitatory effect lay beyond the limits of the conventional receptive field, a 2.5 deg wide strip of the rear projection screen was masked. The masked strip was aligned in visuotopic space with the neuron's excitatory discharge center and aligned in the orientation domain with the neuron's optimal orientation tuning. The mask did not extend into the 4 deg diameter central mask, which was left to shield the receptive field with whatever adequacy it had before. Modulation of remotely-driven inhibition was abolished (preferred direction motion) or nearly abolished (non-preferred direction) by covering this co-axially aligned, co-oriented area of the visual field lying beyond the limits of all conventional receptive field areas (Fig. 2B). This demonstration in a supragranular simple cell (the first cell studied in that penetration) was confirmed in a subgranular B-type cell.

In addition to eliminating modulation by masking a coaxial strip of the visual field, stimulation of a 3.5 deg wide coaxial strip was also tested in the presence of activated discharge. The B cell was excited, although to less than one-fifth the discharge level obtainable with a conventional central stimulus. This observation of an increase in response establishes the existence of remote facilitation. Remote facilitation of activated discharge was observed in 8 of 40 cells (e.g., Fig. 3A, 3C) and was more than 30% above control levels of activated discharge in 3 cells. Responses were averaged for up to 600 sweeps and control periods for baseline response level determination were long (e.g., half the data collection period, Fig. 2). Standard deviations around mean response levels were calculated for each control and experimental region of every response, and were typically 10% of mean levels. Therefore a 23% response increase would be significant at the 1% level of confidence.

In 13 other cells, remote stimulation produced only modulation of inhibition as grating bars passed the point of alignment with the receptive field center. When only modulation occurs, it is possible that the same facilitatory mechanism is operating, but at too low a level to cause frank excitation. Additionally there may be coaxial

modulation of inhibition mechanism (not facilitation), as the response from 6 to 8 seconds in Fig. 2 suggests.

The orientation selectivity of the co-axially aligned disinhibition was tested by varying the orientation of the adapting field in 8 cells that gave a modulated response (see Fig. 3). All showed a remote disinhibitory effect with the orientation selectivity matched to within 5 deg to the cell's optimal stimulus orientation (mean, 2.6 deg). The spread of the remote disinhibitory effect within the orientation domain assumed two patterns. The remote input could be narrowly tuned and impressed upon an accompanying orientation domain inhibition function, which spans 180 deg of orientation (Nelson & Frost, 1978). Two cells displayed this pattern; one is shown in Fig. 3B. The remote input is disinhibitory; the half-width at half-height of the facilitation tuning curve was within 4 deg of the conventional orientation tuning curve's sharpness in these cells. For the remaining cells, the tuning curve was largely free of inhibition so that instead of mere disinhibition, facilitation was observed, at levels above the control responses elicited by the activated discharge bar alone (Fig. 3A,C).

In sum, the remote inhibition spreads broadly in the orientation domain, while the disinhibitory process spreads broadly in the spatial domain, but is sharply confined in orientation. The level of disinhibition reaches facilitatory levels in a minority of cells.

Figure 3 about here.

DISCUSSION

Receptive fields are not big enough

The suggestion has been made that long-range clustered axonal arborizations or other fibers contributing to banded markings innervate classic receptive field areas (Gilbert & Wiesel, 1983; Mitchison & Crick, 1982; Wiesel & Gilbert, 1983), rather than giving rise to novel facilitatory effects. This receptive field role for long intrinsic fibers may be evaluated by quantitatively measuring receptive field extent. Axon lengths of 4 (Gilbert & Wiesel, 1983) to 6 mm (Gilbert & Wiesel, 1982) have been reported. From the data of Tusa et al., (1978) it may be calculated that a 6 mm axon in Area 17 of cat visual cortex would connect points with a retinotopic separation of 3 deg in the area centralis projection, and 6 deg or more at a 5 deg eccentricity, typical of the moderate eccentricities at which most published data arise. How do receptive field sizes compare? Much of the required information is available in the literature; I additionally determined receptive field widths from statistically processed activated discharge profiles (Fig. 1 and Nelson & Frost, in prep.).

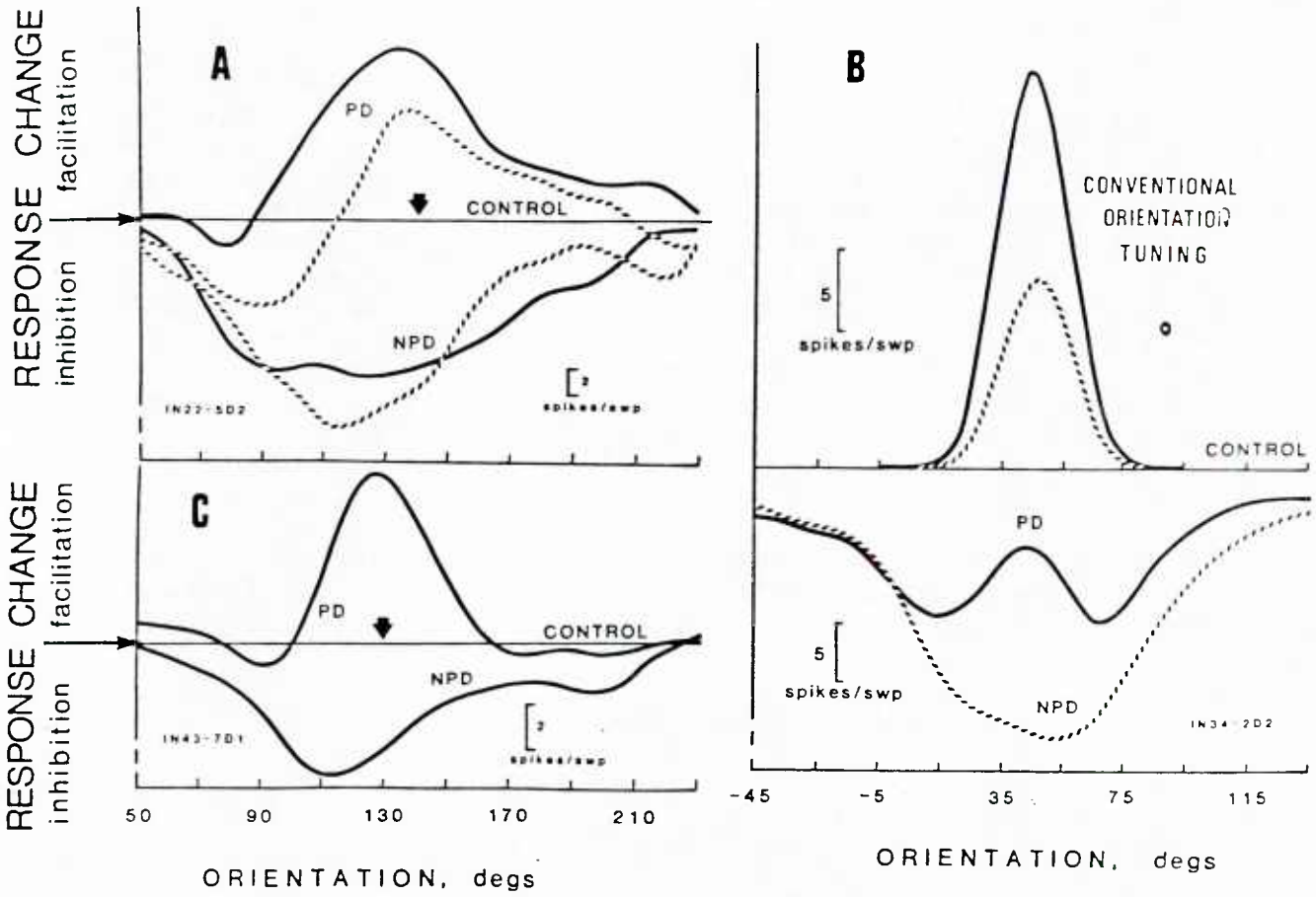

Fig. 3. Remote inputs to three simple-type striate neurons are orientation selective. (A:): Large striped pattern presented beyond receptive field components and moving in the direction-selective cell's preferred direction (PD) facilitate response from a centrally presented, conventional stimulus above **CONTROL** level observed in the absence of peripheral stimulation. Stripes moving in non-preferred direction (NPD) inhibit response (curves below **CONTROL** level). The facilitation is even greater with more of the receptive field region masked (solid curves, 5 deg diameter mask; dashed curves, 3 deg mask). Arrow, optimal orientation for central excitatory response. Maximum inhibition, 65%. (B:) Orientation selective pattern in which remote disinhibition is impressed upon (modulates) broadly-tuned orientation domain inhibition (PD). Disinhibitory peak and sharpness are well-matched to conventional excitatory orientation tuning curve (top). Same neuron as Fig. 1. Total receptive field width including inhibitory sidebands, 5.5 deg; region masked from adapting field stimulation, 10 deg diameter; adapting field, 47 deg diameter, 0.33 cycles/deg, moving at 2.5 deg/sec. Maximum inhibition, 64%. (C:) Orientation selective pattern in which facilitation (PD) is mixed with little inhibition at remote orientations. Excitatory peak width, 0.8 deg; total receptive field width, 3.68 deg; mask, 5 deg diameter. Arrow: optimal orientation for central excitatory response. Adapting field 26 deg diameter, 0.6 cycles/deg. Maximum inhibition (NPD), 46%.

Length of excitatory area. Receptive field lengths of simple cells are much longer when measured by quantitative methods than by hand-plotting techniques. Cells which average 0.18 x 0.52 18 deg in hand-plotted width and length will average 0.79 x 6.41 deg with computer-averaged length-summation measurement (Kato et al., 1978; over 30 cells for all measurements except quantitative length, for which N = 16; maximum length, 10 deg; nearly all cells within 5 deg eccentricity). The difference in length estimate arises from the great deal of spatial summation in excitatory discharge center response (Rose's "facilitatory flanks," 1977), as revealed by quantitative length-response (length-summation) methods using a bar of increasing length. Hand plotting methods yield a form of length-activity profile. Even automating this method yields length estimates of only 2.1 deg (Bishop, Maske & Yamane, personal communication; 15 simple cells, fixed length probe bar typically 0.5 deg long). The excitatory region is a smooth extension of the classic excitatory discharge center. If this center is modeled with the best-fitting Gaussian profile, such length-response curves may be generated by integration of the profile (Henry, Goodwin & Bishop, 1978), albeit with some departures in the form of saturation, end-zone inhibition, and other nonlinearities due partly to the use of response rather than sensitivity measures. The axial facilitatory region appears on some length response curves as a long, trailing input (excitatory) region (Fig. 1.1, shaded area), which does not fit a Gaussian model.

Length of hypercomplex cells. For cells in the simple family with hypercomplexity, two inhibitory areas as well as the central excitatory area must be considered in measurements of length. For 24 cells nearly all within 5 deg eccentricity, the maximum lengths observed for excitatory and inhibitory areas were 3.6 and 4.0 deg respectively. Average overall length of the combined receptive field regions was 5.2 deg (Orban et al., 1979b).

Length of complex cells. Spatial integration functions for complex cells saturate quickly, so that the maximum excitatory length revealed by length-response curves is less for complex cells (range 1.6 - 6.6 deg, mean 4.35 deg, N=6) than for simple cells, and even less when hypercomplexity is present (range 0.7 - 3.6 deg, mean 1.55 deg, N=10; Kato et al., 1978). Activity profiles, in which a small optimal bar traverses a succession of axes passing above, through and below the receptive field, might in future reveal a greater receptive field extent.

Comment. The excitatory discharge areas of end-stopped simple and complex cells are too short to be innervated by neurons with long clustered axonal arborizations. The length of the excitatory discharge center in simple cells without end-stopping fades very gradually and so is marginally long enough. The center's smooth, unimodal and typically Gaussian activity profile seems poorly matched to a substrate with periodically clustered arborizations. Insufficient data are available for complex cells.

Receptive field width. The width across the receptive field excitatory discharge center has been reported as just under and over 1.0 deg for X and Y stream simple cells respectively (Mustari et al., 1982; X-stream range, 0.4 - 1.6 deg, mean 0.94 deg, N=14; Y-stream and layer 6, 0.6 - over 2.7, mean 1.63 deg, N=38). B-like periodic silent simple cells have a maximum excitatory width of 3 deg (8 cells, mean 1.8 deg; Kulikowski & Bishop, 1982).

To obtain the total receptive field width, one must go beyond the excitatory discharge center to the flanking inhibitory sidebands. This was done with the activated discharge method. Taking care to follow the sidebands out to inhibitory

levels of vanishing statistical significance (alpha level, 0.1%), mean widths were as follows: simple cells, 2.9 deg (range 1.16 - 5.5 deg, N=45, 90% with eccentricity less than 6 deg). Complex cell average width is 3.9 deg (range 1.4 - 7.6 deg, N=23, 90% with eccentricity less than 5 deg). B cells had intermediate widths averaging 3.4 deg (N=7, all with eccentricity less than 5 deg).

The wider simple cells were mostly bimodal, with the two excitatory discharge peaks separated on average by 0.84 deg (range 0.5 - 1.6 deg, N=15). The wider complex cells were mostly units with periodic profiles (Pollen & Ronner, 1975).

Comment. The inhibitory margins of simple and B cells are marginally wide enough to be innervated by neurons with long clustered axonal arborizations. However, the inhibition lacks orientation tuning (Bishop et al., 1973; Orban et al., 1979b) or ocular selectivity (Kato et al., 1981). Therefore the inhibitory areas do not require innervation from a system capable of selectivity within orientation and ocular dominance columns. Clustered periodic arbors might be responsible for all the ON areas, or all the OFF areas (but not both ON and OFF areas from the same axon) in cells with multiple discharge centers. But the discharge center area in bimodal simple cells and B-like silent simple cells are too closely spaced. Among complex cells, field width is marginally great enough to be innervated by axons with long clustered arborizations. The multiple peaks of Pollen & Ronner's (1975) periodic complex cells are one receptive field feature which might arise from clustered axonal arborization.

General discussion

In this project, a highly specific input driven from beyond the classic receptive field has been demonstrated in cat striate cortex. The visuotopic area giving rise to the effect exceeds the total scatter in cortex of arriving retinogeniculate fibers (Albus, 1975). The specificity of the effect, especially for orientation, suggests a cortical origin. As classic receptive field components were covered and did not contribute to the measured effects, intracortical pathways are implicated. Intrinsic fibers responsible for the effect would have to follow a preferential interconnection rule singling out neurons whose optimal bar stimuli are both **co-oriented** and **co-axially aligned.** Thus, one of the two hypothetical interconnection schemes proposed on anatomical grounds and modeled by Mitchison & Crick (1982) has been functionally demonstrated in cat. The observed effect was always facilitatory. Preferential interactions propagated from beyond classic receptive field components, but orthogonal to optimal stimulus orientation, were not observed. Using multiple electrode cross-correlation techniques, Michalski, Gerstein, Czarkowska & Tarnecki (1983) have provided a direct, functional demonstration of intracortical connections spanning 1 mm and presumed to be inter-columnar; coupled cells were tightly matched in orientation tuning.

This position-specific facilitatory effect may be related to the phase-specific interactions between pairs of gratings observed in 17 of 38 simple cells by De Valois & Tootell (1983), although it was not determined whether those interactions originated with classic receptive field components or from regions beyond them. The facilitation observed in this project in at least a quarter of Area 17 simple cells in anaesthetized cat is a likely mechanism for the response to subjective contours (Kanizsa, 1976) reported by von der Heydt, Peterhans & Baumgartner (1984) in awake monkey Area 18. The existence of such facilitation had been suggested (Nelson, 1975, Figs. 8, 17).

Remote **inhibitory** effects are more common (indeed, nearly universal: cat striate neurons: Nelson & Frost, 1978; other areas, Grünau & Frost, 1983; pigeon optic tectum, Frost, 1978) and also display orientation selectivity matched to the test neuron's optimal orientation. But inhibition broadly spanned the entire orientation domain (180 deg) and is not selective in the spatial domain. Facilitation is co-axial in the spatial domain and co-oriented in the orientation domain, with a tuning half-width at half-height scarcely broader than conventional orientation tuning curves.

The spatial range and stimulus selectivity of the remote facilitatory effect would be well served by the long, clustered axonal arborizations recently demonstrated by Gilbert and Wiesel (1983), while most classic receptive field components are poor targets. As receptive fields are small and stimuli are large, the facilitation reported here could usefully augment the common response of a population of neurons to the edge of an everyday object. Indeed, there is much to do in vision which transcends the confines of a receptive field. This includes processing for globality in stereopsis, namely drawing out the correct retinal disparity (depth) signal from the clutter of disparity noise (Nelson, 1975, 1977), and ordering the cortex itself into columns and slabs (Swindale, 1982) in order to facilitate yet further, orderly intracortical interactions.

CONCLUSION

Intracortical inhibition (Nelson, Final Technical Report for Contract No. N62269-81-C-0279, "Intracortical Interactions for Orientation Contrast") and facilitation (this Report) have now been demonstrated. These are the twin mechanisms of figure synthesis. A better understanding of how these mechanisms are employed as the cellular basis of perception now waits on better visual stimulation and recording facilities. For example, stereoscopic mechanisms call for double the number of projection channels.

At the same time that the door to higher perceptual function has opened, structure-function relationships in the substrate below have become more intertwined. Possible roles of columnar structure as a shaping force for intracortical interactions have been discussed by Nelson (1985). Descriptions are now available of columns (slabs), and of intracortical interactions. Data are needed which reveal the relation of the two. The origin of the interactions described here--the specific cell-by-cell wiring--can only be resolved with multi-electrode studies. With at least two electrodes, cross-correlation analysis can document input-output couplings between pairs of neurons. This information would go beyond establishing the existence of the interactions to reveal how they arise. Knowing "how" is a prelude to ascertaining "where," and here too multiple electrode techniques are potentially useful. With large electrode arrays to sample the cortical surface, columnar organization can be resolved. For example, clusters of like-tuned cells can be discovered from the pattern of responses on the various electrodes. Then, when one neuron is studied with a particular electrode from the array, the neuron's columnar membership will be known. The way in which columnar membership shapes a neuron's horizontal links can be determined. Such studies will now be undertaken with the 19-channel electrode arrays and cross-correlation instrumentation developed in the Dept. of Physics at Philipps University, Marburg, Germany.

PUBLICATIONS FROM THIS PROJECT

Contracts from the Naval Air Systems Command have supported two electrophysiology laboratories, one studying visual performance in man with the swept evoked potential; and the other, the basis of visual perception at the cellular level, using microelectrode techniques in animals. Support from the Naval Air Systems Command has made the following publications possible and is gratefully acknowledged:

*Nelson, J.I., Kupersmith, M.J., Seiple, W.H., & Carr, R.E. (1984). The swept display technique: separation of X- and Y-dominated evoked potentials. In R. H. Nodar & C. Barber, eds., Evoked Potentials II: The Second International Evoked Potentials Symposium. Boston: Butterworths, 1984, pp. 123-134.

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*Kupersmith, M.J., Nelson, J.I., Seiple, W.H. & Carr, R.E. (1984). Electrophysiological confirmation of orientation-specific contrast losses in multiple sclerosis. Annals NY Acad Sci. **436**: 487-491.

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*Nelson, J.I. & Frost, B.J. (1985 in press). Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex. Exp. Brain Res.

Nelson, J.I. & Seiple, W.S. (in prep.) Evoked potential assessment of human contrast modulation sensitivity under X- and Y-type stimulus conditions.

Invited chapters in the following books

"Unsolved Problems in the Cellular Basis of Stereopsis," in J.D. Pettigrew, W. R. Levick and K.J. Sanderson, eds., Visual Neuroscience, Cambridge U.P. (in press).

*"The Cellular Basis of Perception," in D. Rose and V. Dobson, eds. Models of the Visual Cortex, Chichester: Wiley, 1985, pp. 108-122.

Chapters on the sensory adaptations in strabismus entitled
"The Cortical Basis of Binocularity and Amblyopia" (submitted),
"Binocularity and Vision Loss in Amblyopia" (submitted),
"Disparity Detection and Anomalous Correspondence" (in prep.) and
"Development of Binocular Vision" (in prep.) in Keith Edwards & Richard Llewellyn, eds., Textbook of Optometry, Butterworths (in prep.).

*NAVAIR support cited in Acknowledgements; reprint enclosed.

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